

## 16 Some Mechanisms Producing Structure in Natural Communities: a Model and Evidence from Field Experiments

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### Introduction

#### Community Structure and Niche Theory

If a local assemblage of organisms is to be regarded as a community with some degree of organization or structure, then it is in the interactions between the organisms that we must look to provide this structure. Two different interactions provide most of the organization: competition and predation. I will use competition in the sense of Birch's (1957) first meaning: "Competition occurs when a number of animals (of the same or of different species) utilize common resources, the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or another in the process." I will use predation in the broad sense of an animal's eating another organism for its main source of food, including herbivores that eat plants as well as parasites or pathogens that eat their host.

Predation represents the interaction between trophic levels, whereas competition mainly represents interactions within trophic levels (although if space is the resource, it is possible for plants to compete with sessile animals in aquatic habitats). These two interactions may themselves interact: the numbers of two

competing species may be reduced by their predators to such an extent that competition is prevented. In addition, the physical environment affects the intensity of both sorts of interactions, and the organisms affect the physical environment.

In studying community structure, one aspect of current interest is the theory of the ecological niche. One speaks of how niches are packed together, how much niches can overlap, what determines the breadth or shape of niches, etc. In these discussions the emphasis has been on only one of the two major interactions, competition, because of the way in which Hutchinson (1958) formally defined the niche. In his definition, the boundary of the "fundamental" niche is determined by the limiting states of all possible ecological variables, both physical and biological, which permit a species to exist indefinitely. The "realized" niche is defined as that portion of the fundamental niche within which a species is constrained by interactions with its competitors. "Interaction of any of the considered species is regarded as competitive in sense 2 of Birch (1957), negative competition being permissible, though not considered here. All species other than those under consideration are regarded as part of the coordinate system" (Hutchinson, 1958). Competition under sense 2 of Birch (1957) includes, in addition to the item in his

meaning quoted earlier, "an additional item, namely the interference with one species by another (with consequent change in birth rate or death rate) even when there is no demand for a common resource of space or food. But they exclude predation in which one animal eats another for its main source of food."

Vandermeer (1972) has pointed out that the idea of the niche presented by Grinnell (1917, 1928) is close to the idea of the fundamental niche, since he thought of it as "the concept of the ultimate distributional unit, within which each species is held by its structural and instinctive limitations." This concept of the niche excludes interactions with other species, both competitors and predators. In contrast, Elton's (1927) definition ("the 'niche' of an animal means its place in the abiotic environment, its relation to food and enemies") is closer to the realized niche, since it includes interactions with other species.

The distinction between fundamental and realized niches is a very useful one: if communities are organized by interactions, then the manner and degree of that organization will be reflected in the differences between the sizes and shapes of realized and fundamental niches.

The modern theory of the niche, as proposed by Levins (1968) and MacArthur (1968) and recently summarized and extended by Vandermeer (1972), is based upon the original definitions of Hutchinson (1958).

Vandermeer categorizes Hutchinson's distinction between fundamental and realized niche as a distinction between a

preinteractive and a postinteractive niche (Vandermeer, 1972, p. 109), thus restricting the meaning of interaction to competition. This is also shown by his statement that the species ("operational taxonomic units") have only density-dependent feedback effects on each other and by his equating of "operational habitat" with "resource."

Thus, both in Hutchinson's original definition and in Vandermeer's recent summary and extension of the theory of the niche, only competitive interactions are considered. Other interactions, notably predation, are included in the factors bounding the fundamental niche, in the "conception of the niche as being preinteractive—the potential area within which a species can live as opposed to the area in which one actually finds it" (Vandermeer, 1972). Here, as elsewhere in discussions of niche theory, "preinteractive" means all aspects except competition, and "postinteractive" means "after competition occurs."

In this chapter I would like to challenge the idea that competition is the sole or even the principal mechanism determining the area in which one finds a species, as opposed to the potential area within which it can live. If this is not the case, then the formal structure of "niche theory" needs to be extended so that interactions other than competition are regarded as also constraining the realized niche.

Of course, it has long been recognized that predators can keep potential competitors so rare that they do not compete. Darwin's (1859, p. 67–68) experiment is

probably the first demonstration of this: "If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the more vigorous plants gradually kill the less vigorous, though fully grown plants; thus out of twenty species growing on a little plot of mown turf (three feet by four) nine species perished, from the other species being allowed to grow up freely." Hutchinson (1961), Paine (1966), and Connell (1971) have suggested the same thing, and MacArthur (1972) states: "If abundant predators prevent any species from becoming common, the entire picture changes. Resources are no longer of any concern and our Eqs. (1) and (2) are irrelevant. More correctly, resources are still a concern, but their manner of subdivision is irrelevant." The question I would like to try to answer is, when does predation, or any factor other than competition, limit the distribution or abundance of a species and so affect its role in community structure? Under which conditions does competition determine the shape and size of the realized niche and which not?

#### A Note on Methods

I will first consider the problem of how to detect and measure the extent of biological interactions such as competition or predation. In my opinion this has been the main stumbling block in testing the validity of models of community structure. There seem to have been at least three general methods used to detect or measure biological interactions under natural con-

ditions. The first is to describe the pattern that exists at a point in time to see whether it does or does not conform to the predictions of the model. Some examples of this are gradient analysis (Whittaker, 1967, 1970; Terborgh, 1971), fitting relative abundances to various mathematical models (MacArthur, 1960; Whittaker, 1965; Levins, 1968), and examining the distribution patterns, food habits, etc., of closely related species to see how much their niches overlap. This method is very useful in detecting patterns and suggesting hypotheses for testing.

The second approach is an attempt to apply the experimental method but without using controls. It consists of searching for a "natural experiment." For example, if two similar species occupy the upper and lower halves of a mountain, respectively, with little or no overlap, one hypothesis is that they exclude each other by competition for resources. To test this hypothesis, one looks for a nearby mountain where one or the other is missing (e.g., Diamond, Chapter 14, Figure 39). If competition determines the boundary, the species present should extend beyond the boundary on this second mountain. The trouble with such "natural experiments" is that an essential part of all true experiments is missing: a control. There is no certainty that the only difference between the two mountains is the absence of one of the species. A predator may have been absent, or an essential food organism, soil nutrient, etc., may have been present beyond the boundary on the second mountain.

The third and, in my opinion the best, method for revealing the extent of biological interactions is the controlled field experiment, whose essential aspect is that everything varies in the same way between treatment and control except for the factor being tested (see review by Connell, 1974). In the example above, instead of looking for a mountain with one species missing, one finds another with both species in the same arrangement and then removes one species. The most efficient thing would be to remove it near the boundary; if the other species extends its range into the vacant territory, competition is the most likely mechanism producing the original boundary. If not, the hypothesis can be rejected forthwith.

Such field experiments need careful design. The trick is to make sure that all environmental factors, except the one being tested, vary in the same way and to the same degree on both experimental and control sites. Since there are bound to be some differences, replication is essential. Often it is more difficult to arrange adequate control sites than to perform the treatments.

The effect of the experimental treatment itself must be taken into account. The simplest treatment, removal of one or more species, is probably the best. Alternatively, animals are sometimes introduced into pens or cages (Jaeger, 1971; Wilbur, 1972; Grant, 1972). This may cause problems. First, if emigration is the usual result of aggressive encounters, this will be prevented and unusual outcomes may ensue (Krebs, Keller, and Tamarin,

1969). Secondly, other species of competitors or predators, which would normally have influenced the outcome, may be excluded. If enclosures must be used, these and other such effects need to be taken into account in the final interpretation of the experimental results.

The superiority of such controlled experiments to "natural" ones seems obvious, yet field experiments are rare in all ecological literature. One reason is that it is very difficult to change the abundance of large or highly mobile animals such as birds or large mammals. Also, tradition dictates that experiments are done in laboratories, whereas ecology is done outdoors. Field trials are relegated to agriculture or forestry, and ecology students seldom take courses in these areas. But applied scientists need answers, and necessity stimulated the development both of statistical techniques and of field experiments. Most ecologists have adopted the former but not the latter, to their cost.

In the following section I present a review of the evidence of where competition occurs in natural communities and where it is prevented by predation or physical conditions. The aim of this review is to see whether there is any pattern in the occurrence of competition. I have used evidence from controlled field experiments whenever possible, both to illustrate their value and to suggest where they could be used in the future. Although the number of instances where field experiments have been used are few, they differentiate between the alternatives clearly in a way that correlations between abundances,



gradient analyses, maps of distributions, etc., cannot do.

### The Pattern of Occurrence of Competition

#### Where Is Competition Common Under Natural Conditions?

*On land.* Competition between the roots of canopy trees and those in the understory was demonstrated long ago by controlled field experiments in natural forests in temperate latitudes. Trenches were dug around plots, cutting all roots and so eliminating competition for water or nutrients with adult trees (Fricke, 1904; Toumey and Kienholz, 1931; Korstian and Coile, 1938; Lutz, 1945; Shirley, 1945). In every case the smaller trees inside the trenched plots survived and grew much better than in nearby control plots. In the one published instance of trenching in a tropical forest, the plants in the experimental plot did not do better (Connell, 1971). This may have been due to the greater competition for light in this very dense forest and/or to a greater intensity of grazing.

Interference between bushes and herbs in the chaparral vegetation of California has been demonstrated in several studies. In laboratory experiments the bushes have been shown to contain volatile or waterborne chemicals that inhibit germination and early growth of herbs (Muller, 1966). New plants become established mainly after fires, which destroy the "allelopathic" effects of the original vegetation. However, as will be discussed later, graz-

ing may also affect seedling establishment in chaparral.

Direct evidence of interspecific competition between animals comes from field experiments on vertebrates and social insects. When DeLong (1966) reduced the numbers of the meadow mouse *Microtus*, the population of house mice (*Mus*) increased as compared to that on a control area. This increase was not due to greater growth or survival of adults, but rather to a greater production of young. This was probably due to lack of disturbance by *Microtus* of nests of *Mus*, since, in the laboratory, female *Mus* either deserted their nests or ate their young in the presence of *Microtus*. In another field experiment Koplin and Hoffman (1968) found that competition probably determined the spatial distribution of two species of *Microtus*. During a summer's trapping *M. montanus* was never caught in the wetter parts of the habitat where *M. pennsylvanicus* lives. Over the subsequent autumn and spring *M. pennsylvanicus* was systematically removed, greatly reducing its density. Then *M. montanus* was caught in the wetter places for the first time. Unfortunately the population densities of both species on the control area were much less than on the experimental area. Therefore, the fact that *M. montanus* were never caught in the wetter habitats on the control plot may have been the result either of the very small sample size or of the lack of intraspecific pressure to explore new areas, rather than from competitive aggression by *M. pennsylvanicus*. Apparently these two studies are the only field experiments on interspecific competition

in rodents in which any sort of control area was established. Grant's (1972) review cites other field experiments that did not use control areas.

To my knowledge, the only field experiment testing for the existence of interspecific competition in birds is that of Davis (1973). By trapping over a period of three years in a field bordered by trees and bushes, he found that most of the golden-crowned sparrows were feeding both on seeds and young plants along one particular portion of the edge. Juncos, which feed almost entirely on seeds, occurred more or less equally around the edge of the field. In the fourth year he removed almost all the sparrows within two months. For the next two months, in the absence of the sparrows, a high proportion of the junco population shifted into the portion of the field where most of the sparrows had been feeding. Then half of the captured sparrows were returned to the field and the other half released 0.64 km away; about half of these reached the field within a week. Again a high number were found along the same portion of the edge where they had been commonest before. Concurrently the proportion of the total junco population in that area fell back nearly to the size it had been before the sparrows were removed. Although no separate control area was established, the fact that the junco population rose when the sparrows were removed and fell quickly when they were returned is strong evidence that the sparrows were excluding the juncos from that part of the habitat.

Other experimental evidence of compe-

tition between vertebrates comes from populations confined in pens. Jaeger (1971) found two species of salamanders occupying adjacent habitats. The first species, which normally lived only in shallow soil, survived well in pens in areas with deep soil, if the second species from the deep soil was excluded. However, if the species were penned together, the first survived poorly. No aggressive behavior was ever seen in the laboratory and the mechanism for this apparent competition is unknown. The number of animals used was small and the effects of the pen are unknown; manipulation of large numbers without using pens would be a welcome extension of these interesting experiments.

A series of controlled experiments with rodents in large pens has been done by Grant (see his review, 1972). He showed that each species was restricted to one type of habitat by competition with another species. These were mice which mainly used the surface of the ground rather than burrowing or climbing, so that they were likely to be competing for space.

Field experiments on competition between ant colonies have been done in at least two instances. Brian (1952) set up artificial nest sites by placing slabs of stone or slate on the ground or building turf banks. Initial colonization by different species was "near random," but then certain species were observed to drive out other species by direct aggression or to move in when the other species had left during a drought or cold spell. Pontin (1969) moved whole colonies into new positions. The colonies left behind, being less crowded, often produced more alate

queens in the next two years. In the colonies that were more crowded after new colonies had been moved adjacent to them, fewer queens were sometimes produced. These effects were apparently more drastic on other colonies of the same species than on those of different species.

In the absence of experimental manipulation, observations of aggressive displacement of one species by another are convincing evidence of competition. For example, Way (1953) observed one species of ant gradually driving another species back through a coconut plantation in Tanzania. Levins, Pressick, and Heatwole (1973) observed aggressive interactions between different species of ants when bait was placed on the ground on small Caribbean islands. Aggressive displacement of one species by another has also been observed in birds (Pitelka, 1951; Orians and Collier, 1963; Orians and Willson, 1964) and mammals (Brown, 1971; Heller, 1971; Sheppard, 1971).

Indirect evidence of interspecific competition comes from observations of non-overlapping adjacent ranges (Diamond, 1973), inverse correlations of abundance (Brown, Chapter 13), niche shifts on islands where competitors are absent (Crowell, 1962; Diamond, 1970 and Chapter 14), character displacement, etc. Such indirect evidence is open to explanations other than competition.

*In aquatic habitats.* Benthic invertebrates in fresh-water lakes sometimes occur at such high densities that they probably compete for space or food (Jonasson, 1971). Reynoldson and Bellamy (1971) have performed a field experiment

which indicated that one species of flatworm was able to displace another in a small lake in Wales.

Wilbur (1972) enclosed populations of various combinations of six species of amphibians in pens along the edge of a pond. Competition occurred among the three local species of salamanders, affecting survivorship, length of larval period, and body weight. A fourth species not occurring locally was introduced; it survived well alone, but competed with the local species if grown with them. Another species of salamander was also a competitor unless it was able to grow quickly to a larger size, when it apparently became a predator on the other salamanders. Having frog tadpoles as prey may have given it this advantage of faster growth. To carry out these complex experiments it was necessary to enclose the populations in pens. These excluded other species of predators, both invertebrate and vertebrate, which probably would have affected the outcome of the interactions under natural conditions. However, this study is one of the most complete and rigorous analyses of the complex interactions that produce structure in communities.

Several controlled field experiments have demonstrated the existence of interspecific competition in marine organisms. The usual procedure consists in changing the abundance of one species and observing the survivorship or growth of another, with adjacent controls. All of the experiments have been done on rocky seashores. Connell (1961b) found that one species of barnacle was eliminated from lower shore zones by another that grew faster and

either smothered, crushed, or undercut the first. Haven (1966, 1973) changed the population density of two species of grazing limpets and found that they affected each other's growth rates. A similar instance of competition for food between two predatory starfish was demonstrated in a controlled field experiment by Menge (1972). Competition for space producing a nonoverlapping mosaic between two species has been demonstrated with limpets by Stimson (1970, 1973) and with barnacles and anemones by Dayton (1971). Observations also suggest that competition may occur between barnacles and attached algae (Dayton, 1971).

#### Where is Competition Prevented by Predation?

*On land.* Much of the experimental evidence for predation as an important factor in community structure deals with predation on plants by mammals. Grazing by wild rabbits kept grasses from displacing dicotyledonous herbs in southern England. When rabbits were excluded by fences, or after they had been eliminated by an epidemic of myxomatosis, grasses invaded, forbs disappeared and woody vegetation began to invade (Tansley and Adamson, 1925; Hope-Simpson, 1940; Watt, 1957, 1960; Thomas, 1960). When mice and voles were excluded with fences for seven years, the same thing happened in a conifer plantation in Wales (Summerhayes, 1941). Experimental exclusion of voles from grassland in California for two years showed that their grazing changed the relative abundance of species, reducing the palatable species (Batzli and

Pitelka, 1970). Thus small mammals, by selective predation, can determine the community structure of terrestrial vegetation.

Another example is the effect of insects on a species of hemiparasitic herb living in the understory of deciduous forests in Michigan. When these grazers were removed, the plant population increased greatly (Cantlon, 1970).

The regeneration of trees may be almost completely prevented by grazing mammals. In three species of trees in the New Forest in England, the populations consist of three "generations," established in the intervals 1648 to 1763, 1858 to 1915, and since 1938 (Peterkin and Tubbs, 1965). The two latter generations coincide with periods when grazers such as deer, cattle, and ponies were removed from the forest. Regeneration is limited to occasional escapes from predation. Once trees get tall enough, they are vulnerable to attack only by insects or pathogens. Instances of complete defoliation by insects, sometimes with mass mortalities of adult trees, have occurred, e.g., balsam fir in Canada (Morris, 1963) and *Eucalyptus delegatensis* in Australia (Readshaw and Mazanec, 1969). As pointed out by Murdoch (1971), balsam fir is vulnerable to this heavy attack only when mature and in continuous even-aged stands, where, presumably, the dispersal of insects on to other vulnerable trees is facilitated.

In the chaparral vegetation in California the competitive interference through release of chemicals (allelopathy) between bushes and herbs is sometimes modified by grazing. The periodic fires which re-

move the allelopathic effects also destroy or drive out the grazing animals (Halligan, 1972; Christiansen, 1973). Either experimental removal of the tops of allelopathic plants or exclusion of grazing vertebrates by cages or fences, or both, has been done in several instances. When vertebrate grazers alone were excluded, herbs have sometimes become established in abundance near allelopathic shrubs (Bartholomew, 1970; Halligan, 1972), sometimes much less abundantly or not at all (McPherson and Muller, 1969; Muller and del Moral, 1971; Chou and Muller, 1972; Christiansen, 1973). The biggest change has been reported when both grazing and allelopathy have been experimentally eliminated together in these studies. The conclusion from these studies is that both allelopathic interference between the plants and grazing by herbivores influence the community structure of chaparral vegetation.

Some field experiments testing the interaction between grazing and competition between grasses and forbs have been done on sheep pastures (Sagar and Harper, 1961; Putwain and Harper, 1970). They indicate that grazing may reduce competition, but without knowledge of whether wild herbivores graze natural vegetation at the same intensity as these sheep did, it is difficult to generalize from these results.

The effect of predators on terrestrial animals has seldom been estimated from field experiments under natural conditions. The only controlled field experiment I know of concerns the effect of woodpeckers on Englemann spruce beetles

(Knight, 1958). The birds concentrate their attacks both in the groves and on the individual trees where the beetles are commonest. By using exclusion cages on 250 trees in the Rocky Mountains, Knight was able to show that the predators caused proportionately greater mortality where the prey were denser. Murdoch (1966) has shown that carabid beetles will survive well through the summer only when protected from predation.

Predators of terrestrial vertebrates do not seem to be so effective in reducing their prey, for reasons which will be discussed later. Predators of ruffed grouse were removed almost completely in two different places; nesting losses were reduced but the adult populations did not increase (Edminster, 1939; Crissey and Darrow, 1949). This supports the suggestion of Levins (Chapter 1) that a change in production of one life stage may not affect the abundance of another life stage limited by some other factor. When about half of the predators of the vole (*Microtus californicus*) were removed during a peak in vole numbers, the population declined to the same degree as it had from a previous peak (Pearson, 1966). The often-cited instance of an irruption of the deer population following the reduction in their predators on the Kaibab plateau of Arizona has been shown to be incorrect by Caughley (1970). There is one instance in which predators have been effective in reducing mammalian populations, i.e., wolves and moose on Isle Royale in Lake Superior. Although no controlled experiments have been done, the evidence strongly suggests that before the wolves

arrived the moose were so dense that their feeding was injuring the vegetation. This is not happening now that wolves are feeding on the moose (Mech, 1966; Jordan Shelton, and Allen, 1967).

*In freshwater.* The zooplankton of open water in lakes without planktivorous fish usually consists of several species of relatively large crustaceans, together with smaller species of various groups. After planktivorous fish have been introduced and increased substantially, the larger species of zooplankton are absent from the open water and the smaller species are much commoner. Several studies have compared the same pond or lake before and after fish were introduced, and all have found that the large species disappeared and the smaller species increased, suggesting that the fish selectively ate the larger zooplankters (Hrabacek *et al.*, 1961; Brooks and Dodson, 1965; Macan, 1965; Reif and Tappa, 1966; Galbraith, 1967; Wells, 1970; Hall, Cooper and Werner, 1970; Warshaw, 1972). Brooks (1968) has confirmed that planktivorous fish selectively eat the larger zooplankton in laboratory experiments, as have Galbraith (1967) and Green (1967) by comparing stomach contents with plankton samples.

Where large aquatic vegetation is dense, the herbivorous zooplankton is much more abundant, even though phytoplankton productivity is less. A likely reason for this is that fish predation is less effective in dense vegetation. Hall *et al.* (1970), found that in ponds with dense vegetation (caused by addition of large amounts of mineral nutrients) the biomass

of zooplankton was not reduced significantly by fish. But in replicate ponds with less vegetation, fish reduced the biomass of zooplankton significantly below that in control ponds.

Other predators besides fish may change the biomass and/or relative abundance of zooplankton. In a series of alpine ponds in Colorado where salamanders (*Ambystoma*) were common, the herbivorous zooplankton species were small. Where salamanders were rarer or absent, larger herbivores occurred (Dodson, 1970; Sprules, 1972). Like fish, salamanders also tend to select the larger individuals as prey, judging by stomach contents and laboratory experiments.

Field experiments on invertebrate predators have been conducted in only one study, by Hall *et al.* (1970). The biomass of zooplankton was consistently lower in treatments with increased invertebrate predation. The predators removed the larger herbivores first, thereby changing the species composition of the community in the same fashion as the vertebrate predators did.

It is difficult to decide whether fish or invertebrate predators have a greater effect on the relative abundance of species in the zooplankton. The field experiments of Hall *et al.* (1970) underestimated the effects of invertebrate predators since a small predator, *Chaoborus*, was left behind in the "reduced" treatment. Dodson (1970) calculated that the predation rate on *Daphnia* by the population of predatory midge larvae was about 10 times that of the salamander population. However, in the experimental ponds of Hall *et al.*



(1970), even with augmented numbers the invertebrate predators did not completely eliminate the larger herbivores as did the fish.

The benthic flora and fauna of freshwater lakes are also affected by predation. Field experiments excluding fish (Black, 1946; Threinen and Helm, 1954) and tadpoles (Dickman, 1968) resulted in rapid growth of larger plants. However, some of the fish were introduced asian carp, which may not have had such devastating effects in their native waters. Experimental removal and addition of fish (*Lepomis* sp.) in ponds or lakes have resulted in a greater standing crop of benthic invertebrates without fish (Ball and Hayne, 1952; Hayne and Ball, 1956), or no change (Hall *et al.*, 1970). This difference may have been the result of the much higher density of fish used in the two former studies (97 and 179 kg/ha, respectively) than the latter (50 kg/ha). Hall *et al.* (1970) found that the fish reduced the larger animals (insect larvae and amphipods), and the smaller species increased, maintaining the total biomass. The fish selected the larger pupae, thereby greatly reducing the numbers of emerging insects.

When invertebrate predators were reduced, the biomass of benthic invertebrates rose, but when these predators were increased, biomass rose in the first summer and fell in the second. Increased predation had predictable effects on the two principal species, the midge *Chironomus* being reduced and the ephemeropteran *Caenis* increasing.

Some experiments and observations have shown that fish may also be affected

by their predators. In lakes and rivers young salmon are heavily preyed upon by predatory fish and birds. Removal of these predators increased the survival to both the smolt and adult stages (White, 1939; Foerster and Ricker, 1941; Foerster, 1954; Elson, 1962). Jackson (1961) observed lakes with and without the large predatory tiger fish (*Hydrocyon vittatus*), which eats all fish small enough to swallow. Only adults of species larger than this occur outside the shelter of aquatic plants in lakes with the tiger fish, but in lakes without it, small fish swim in open water.

In most of these studies, the predators selectively removed the larger invertebrates, regardless of species, and the smaller herbivores usually increased. This is interpreted by most of the authors to indicate that without the larger competitors, the less efficient smaller species could secure more of the limited resources and so increase. However, an alternative hypothesis is that after the predatory fish were added, they removed not only the larger competitors but also the predators of the smaller species. Fish removed the predatory insects in the experiments of Hall *et al.* (1970), and presumably also in some of the other lakes studied. However, when invertebrate predators were added by Hall *et al.* (1970), it is less likely that they ate the predators of the smaller herbivores. Thus *Caenis* increased, almost certainly because its competitor *Chironomus* had been reduced by invertebrate predators. Likewise the larger cladocerans in the zooplankton decreased progressively through the summer, and the rotifers increased. Invertebrate predators, by

reducing the larger herbivores, which are probably more efficient collectors of suspended food (Brooks and Dodson, 1965), probably allowed the less efficient smaller species to increase. However, to elucidate the role of competition properly, field experiments are essential. Sprules (1972) has done a small-scale pilot experiment that indicated that the large *Daphnia pulex* has a deleterious effect on the smaller *Daphnia rosea*. Repetition of this interesting experiment on a larger scale would be welcome.

The effects of grazing by zooplankton on phytoplankton has recently been estimated by Porter (1973). She suspended clear plastic bags holding about 0.5 m<sup>3</sup> of water a short distance below the surface of a lake. The numbers of zooplankton grazers were either reduced, increased, or kept the same in the bags. Counts of the phytoplankton after four days in the bags and examination of gut contents of the grazers showed that some groups of plants were reduced, others increased, and some were unaffected. The growth of some gelatinous green algae may have been increased by passage through the gut of zooplankters (as discussed by Patrick, Chapter 15, for grazing on algae by crustacea), whereas small edible species are reduced. Thus grazing may completely change the relative abundance of freshwater phytoplankton.

Where physical conditions become very harsh in fresh water, predation is reduced. For example, in the alpine ponds studied by Dodson (1970) and Sprules (1972), shallower ones froze to the bottom each winter and sometimes dried up in late summer, whereas deeper ones never did.

The predators in the deeper pools were the axolotl salamander and *Chaoborus*, neither of which apparently tolerates freezing or drying. Both were absent from all shallow pools, where the only predators were a large copepod, which apparently tolerates the harsh conditions, and/or a salamander, which could leave the pond and hibernate elsewhere; this salamander was never as abundant in these pools as the axolotl was in the deeper pools. Thus, predation was probably less intense in harsher conditions.

A second example involves large lakes. The deeper hypolimnion of temperate lakes often becomes anoxic in summer, reducing the activity of fish. Therefore, fish feed less of the year in the deeper than in the shallower depths, which do not become anoxic. Jonasson (1971) found that the midge *Chironomus anthracinus* reached much higher population densities in the hypolimnion than at shallower depths of Lake Esrom, Denmark. Since almost all of the mortality occurred during the short period when the predatory eel (*Anguilla*) could feed, between the autumn overturn and the onset of winter, Jonasson ascribed most of the mortality in deep water to predation. At shallower depths *Chironomus* never attain such high densities, possibly because the predators are able to feed on them for the entire warm season.

Because growth is also inhibited when oxygen is lacking in the hypolimnion, not all the *Chironomus* larvae complete development in one year. However, some do and emerge in May, leaving others behind. But in most years there are so many

left that they still search the bottom completely with their feeding activities and eat all the eggs of their own species that are laid in early summer, thus completely suppressing the next generation. Only after the two-year-olds emerge can a new generation of eggs start to develop in the hypolimnion. In shallow water, growth and development are faster, all emerge at the end of one year, and space is left for a new generation each year. Thus predation thins out the population in shallow depths, but in deeper waters harsh physical conditions (anoxia) exclude predators for a greater proportion of the year. The prey apparently survive these harsh periods so that, with less predation, population density is greater, as is competition for feeding space.

The studies described above have demonstrated the dominant role of predation in determining the relative abundance and distribution of species in fresh-water lakes. The community structure is completely different, depending upon whether fish happen to be present or not. If not, the presence or absence of amphibian or invertebrate predators produces a different community structure. Competition may occur if the intensity of predation is so low that high population densities of herbivores develop.

*In the sea.* On rocky shores in temperate zones, grazers and predators often keep their prey populations so low that competition is prevented. The evidence for this comes from experiments in which grazers or predators were removed. The classic experiment of Jones (1948), who removed 15,000 limpets from a strip of rocky shore, demonstrated the great effect

of these herbivores on abundance of algae. The algae quickly colonized and covered the surface for several years. Others have repeated the experiment elsewhere with similar results (Southward, 1953, 1964; Castenholz, 1961; Haven, 1966, 1973; Dayton, 1970). The same effect of grazing by sea urchins on algae in tide pools or rocks below the intertidal region has been demonstrated by experimental removal (Kitching and Ebling, 1967; Jones and Kain, 1967; Paine and Vadas, 1969; Dayton, 1970). Lastly, by excluding herbivorous fish from intertidal and subtidal areas on coral reefs, Stephenson and Searles (1960) and Randall (1961) have found that they too keep algae and sea grasses grazed down. Unplanned experiments on a larger scale have shown the same effect. Grazers were killed by a spill of fuel oil from a tanker wreck (North, Neushal, and Clendenning, 1964), and by detergents used to clean shores of crude oil (Smith, 1968). Algae colonized and grew profusely after the grazers were gone.

On the middle and lower shore levels experimental removal of predators has shown that they also often eliminate sessile animals before these reach maturity. All barnacles were eaten by predatory snails within 18 months in Scotland (Connell, 1961a) or 12 to 15 months in Washington (Connell, 1970; Dayton, 1971) and New Zealand (Luckens, 1970), except where predators were excluded by cages. Mussels survived only in cages (Connell, unpublished; Dayton, 1971) or when the predatory starfish were picked off by hand (Paine, 1966, 1971).

Yet despite this very heavy grazing and

predation, some plants and sessile or sedentary animals survive to maturity and live a long time at low shore levels. The clue to how this happens is in the age structure of these populations: they often consist of widely spaced older year-classes. I have studied in detail the population dynamics of one such species, the barnacle *Balanus cariosus* on San Juan Island, Washington (Connell, in preparation). At the start the population consisted of classes aged 2, 4, and at least 10 years. Over the next 13 years, snail predators ate all the young that arrived every year at two different study sites, with three exceptions: once at one site and once at each of two different shore levels in different years at the other site. In these instances some individuals survived to the age of 2 years, at which time they were invulnerable to all the common predators except the very large starfish *Pisaster ochraceus*. I tested the invulnerability to smaller predators by protecting the barnacles in cages for varying lengths of time and then removing the cages or allowing predators to enter. All *B. cariosus* younger than 2 years were quickly eaten, whereas only seldom were older ones eaten. Dayton (1971) has since confirmed these findings.

As described earlier I have found that, under natural conditions, *B. cariosus* survives to this invulnerable age only occasionally, so that the populations consist of "dominant year classes." This age structure is produced by occasional escapes from the intense predation to which they are usually subjected.

Other organisms may also reach a size at which they are invulnerable to predators. Kitching, Sloane, and Ebling (1959)

found that the mussel *Mytilus edulis* became invulnerable to attack by crabs. Only one species of very large crab, *Cancer pagurus*, could break open the larger mussels available. This case is similar to that of *B. cariosus*; the prey can reach a size invulnerable to the smaller species of predators, but there exists a very large species of predator to which it never is invulnerable. Dayton (1971) suggests that *Mytilus californianus* may reach a size at which it becomes invulnerable to *Thais*; although this is probable, no evidence exists, since the predators ate all sizes offered in the experiments.

Some species of intertidal algae may become invulnerable to grazers. Southward (1964, Table 2) found that the alga *Fucus vesiculosus*, which colonized a shore after limpets, *Patella vulgata*, were removed, maintained a complete cover for the next 2 years. During this period many small limpets colonized the rock beneath the canopy of large algae. After 4½ years the limpets were much larger and the algal cover had been reduced to 22%. The smaller limpets evidently did not attack the large algae, feeding instead on the smaller plants that colonized beneath the canopy. When they grew larger, they ate the large algae. It seems reasonable to draw the conclusion that large algae are invulnerable to small grazers but not to large ones.

Grazing and predation are often extremely intense under the more "benign" conditions of the lower shore, and "escapes" to invulnerable size occur only rarely. The only data as to the frequency of such escapes in natural conditions are those I have given for *Balanus cariosus*.

About every 5 years they escape from smaller predators; they may then survive for 15 years or so before being eaten by larger predators.

Where is competition prevented by physical conditions?

*On land.* In certain very harsh deserts, the germination of seeds and the establishment of seedlings of perennial plants may be prevented by the absence of rainfall for many years. For example, in central Australia, *Acacia aneura* produces viable seeds in most years, but no seedlings get established. In the occasional years when rainfall is higher, seedlings may survive longer, but are usually destroyed by insects. Only if at least three successive years of higher than normal rainfall occurs will a crop of seedlings become established; this happens about every 40 to 50 years, judged by the age structure of the trees. Then competition for water between the seedlings ensues, and some may die (Slatyer, 1975). The population of *Acacia aneura* thus consists of widely spaced year-classes, produced by occasional escapes during rare periods of mild weather.

*In aquatic habitats.* Near the upper margin of their distribution in the intertidal zone, marine organisms are exposed for long periods to extreme and variable weather; young colonists are usually killed by the harsh physical conditions. Evidence for this comes from various field experiments in which the conditions were improved at high levels. For example, Hatton (1938), Frank (1965), and Dayton (1971) arranged streams of sea water above the intertidal zone; algae and bar-

nacles survived much higher than usual in these streams. Barnacles survived better under shades set up by Hatton (1938) on the upper shore. Conversely, barnacles transplanted to higher levels quickly died (Hatton, 1938; Foster, 1971); the smaller barnacles died before the larger ones. In general, younger or smaller individuals are more vulnerable to harsh physical conditions. This is probably a consequence of the greater surface-to-volume ratio of smaller individuals; they are relatively more exposed than larger ones to such hazards of the external environment as desiccation, increased radiation, extreme temperatures, fresh water, etc. (Lewis, 1964).

Weather being variable, there will occur periods when the harsh conditions are temporarily ameliorated. If favorable conditions last long enough, the young colonists may reach a size where they can survive the usual harsh weather. Many marine species at higher latitudes have short seasons of breeding and settlement each year, so that such "escapes" may happen only once every few years. For example, out of four year-classes of the barnacle *Balanus balanoides* that I observed at high shore levels, survival was high in only one, so that the population was composed mainly of the survivors of that year-class (Connell, 1961a, Figure 12). Other examples of populations dominated by older year-classes at high shore levels are three species of barnacles studied by Foster (1971) and a limpet, *Acmaea scabra*, studied by Sutherland (1970).

An interesting example for marine algae is given by Kain (1963). The physical conditions in the sublittoral zone de-

teriorate as the light intensity diminishes with depth. At the lower limits of distribution of two populations of the large seaweed *Laminaria hyperborea*, the growth rate and population density diminished, and the age distribution consisted of dominant year-groups. In contrast, the shallower populations showed little evidence of such dominant age groups. Recruitment evidently happens intermittently in the populations near the lower edge of the range. Kain (1963) felt that recruitment occurred only occasionally when the conditions become temporarily favorable, but there is no direct evidence in support of this suggestion.

#### **What Determines When Competition Will Occur?**

The evidence from controlled field experiments on the occurrence of competition and on the instances when it is prevented by predation or harsh weather has now been reviewed. It seems clear that competition is often prevented by predation, less often by harsh physical conditions. In fact, so many instances have been demonstrated by controlled field experiments, in contrast to being simply suggested by correlations, that I suggest the following priority be followed in adopting simplifying assumptions to use in models of community structure.

Predation should be regarded as being of primary importance, either directly determining the species composition or in preventing competitive exclusion, except where the effect of predation is reduced for some reason. There seem to be two

principal situations in which predation is reduced, both the result of evolution of defensive adaptations by the prey.

1. Some prey species have evolved the ability to live in refuges that the predator cannot invade, either because the conditions are too harsh for the predator or the habitat structure too difficult to search. Outside the refuges the prey are eaten, e.g., *Balanus glandula* on the middle and lower seashore or larger zooplankton in open waters. The highest levels on the shore provide a refuge where the predators cannot drill and consume a barnacle during the short period at high tide. In the dense vegetation of ponds the fish cannot effectively search for zooplankton.

There is a great difference in the relative abundance and species composition of the zooplankton or benthic invertebrates in lakes with or without large predators such as fish or amphibians. Large species of zooplankters or benthic invertebrates are eliminated where these large predators are present. These larger invertebrates must have evolved in lakes without fish, and depend for their existence on the fact that these larger vertebrate predators have low rates of movement between lakes and so have not reached many small lakes. Only in recent years have they done so, thanks to the stocking by government fishery departments.

This category of species protected by refuges includes many prey species that are smaller than their predators. They may exist as "fugitive" species, invading isolated patches of habitat such as lakes or islands before their predators, which have lower powers of dispersal. Alternatively, they live in the same habitat but



have absolute refuges from their predators.

Where the prey species are free of predators, they may increase in numbers until they compete for resources with other species. This is the usual explanation for the low abundance of smaller zooplankters in the lakes without large predators: that the larger zooplankters are more efficient competitors. However, the small zooplankters may be more common when fish are present because the fish also remove the predatory invertebrate species, which in lakes without fish reduce the smaller zooplankters.

A cautionary note is relevant here. The number of species is usually lower on smaller or more isolated islands. The fact that species there often undergo "niche shifts" on islands is usually interpreted as being due to the absence of one or more competitors (Crowell, 1962; Diamond, 1973, and Chapter 14, Figures 39–43). But an alternative hypothesis is that a significant predator may also be absent. Clearly, controlled field experiments are necessary to decide between the two alternatives in such instances.

2. In a completely different category are those species that defend themselves against predation by evolving adaptations allowing them to coexist with predators without having to live in refuges. The defenses may be morphological (spines, bark, stinging cells), chemical (tannins, alkaloids), behavioral (aggressive nature, social groups, parental care), or simply growing too large to be attacked successfully.

The problem with most of these defenses, most obvious with the last, is that

they are less effective in younger than in older individuals. Parental care is an excellent adaptation to bridge the vulnerable young stage. Parental care is particularly well developed in groups such as birds and mammals. Having also evolved adaptations such as homeothermy and large size, these animals have escaped many of the hazards of the physical environment and of predation. Thus, it would be expected that their populations might be limited by competition for resources, as is assumed in many of the chapters in this book. A similar conclusion may be reached from consideration of survivorship curves: intraspecific competition among adults is more likely in species in which many young survive to adulthood (e.g., birds and mammals) than in species in which most young perish before adulthood.

In species with little parental care, the young survive until they reach a less vulnerable larger size only when predation is occasionally reduced, as in the case of *Balanus cariosus* described earlier. Once an individual or group survives to a size at which attack by a predator is much less probable, it will continue to grow and hold more resources, suppressing its neighbors or smaller individuals beneath it. Thus, competition involving the larger individuals is to be expected, once they escape their predators. Another advantage of large size is that it renders the individual less vulnerable to extremes of physical conditions. This is attested by dominant year-classes, representing escapes during occasional mild spells, in populations in normally harsh regimes.

An interesting aspect of physical harsh-

ness is that if prey and predator have similar physiological requirements, the prey species can sometimes tolerate physical extremes in which the predator cannot attack it. For example, sessile animals such as barnacles or mussels can survive on the seashore at such high levels that their predators cannot attack them, as described earlier. This relationship obviously does not apply if the two species have different physiological makeups, e.g., a land predator such as a seabird attacking a marine invertebrate.

If we consider only species of prey and predator from the same habitat, it follows that if physical conditions become more harsh, i.e., extreme, variable, unpredictable, or any combination of these, predation would be expected to be reduced.

This category includes the larger plants and animals on land and in aquatic habitats. The large plants and sessile aquatic animals provide much of the physical structure of ecosystems, modifying the climate or water movements and providing the vertical structure inhabited by many smaller species. Therefore a more detailed analysis of the mechanisms determining the relative abundance, distribution, and diversity of these species is in order here.

#### **A Model of the Community Dynamics of Large Sessile Species of Animals and Plants**

Communities dominated by large sessile species are the rule in most terrestrial habitats, and in shallow aquatic ones. Terrestrial plant communities, coral reefs, beds of turtle grass or kelp, oyster reefs, rocky shores covered with large barnacles,

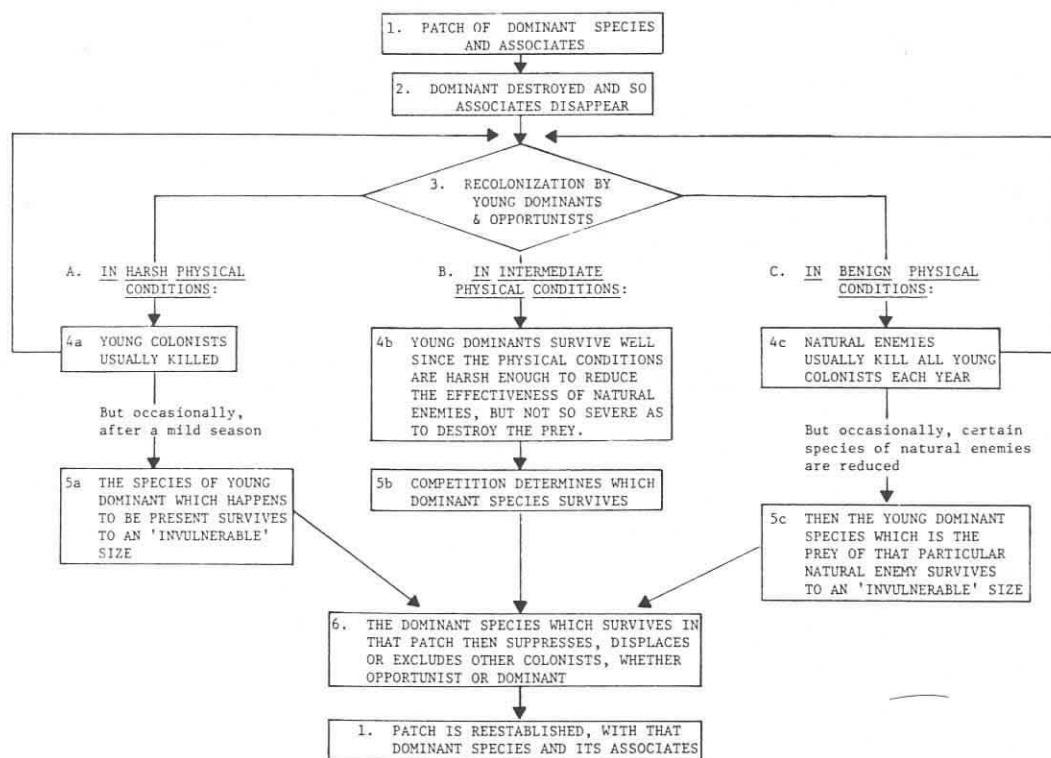
mussels or algae, and the macrophytic vegetations in the littoral of lakes are common examples. All are mosaics of patches of "dominant" species, and gaps are continually appearing as individuals or groups are killed by predators, storms, floods, fires, etc.

The ecological events and evidence described above for marine communities can be summarized in a general scheme, which may serve as a testable model of use in predicting which species of "dominant" succeeds in occupying a gap.

Benthic plants and animals are arranged in a mosaic of patches, some held by long-lived dominants, others inhabited by a mixture of opportunists and young individuals of the dominants. The latter are usually killed within the first year after settlement. Many other species live only in the sheltered conditions created by the dominants. This is the situation shown in Figure 1 as step 1.

Let us now suppose that a patch of dominants is removed, by unpredictable variations in weather, damage by floating objects such as logs, increases in predation, or simply because the large older dominants die as they reach old age. Then the vacant patch is quickly colonized by opportunists, which characteristically have long breeding seasons and numerous motile spores or larvae. In addition, young stages of dominant species that happen to be available may be among the colonists (steps 2 and 3, Figure 1). The events that follow are different in harsh and in benign conditions.

In very harsh conditions, such as at the upper margin of the intertidal zone or in places with much abrasion, most newly



**Figure 1** A model of the mechanisms determining which "dominants" (large plants or sessile aquatic animals) will fill a gap. See text for further discussion.

settled or young individuals are killed by harsh weather each year so that the patch is continually being colonized and vacated; this cycle is shown between steps 3 and 4a. They survive only in particularly favorable years, and then may live a long time. Populations consist of dominant year-groups, the survivors from these occasional favorable years. Because they occupy more and more space as they continue to grow, they exclude and may displace other organisms (steps 5a to 6).

In other words, once two or more individuals are past the vulnerable young stage, they may compete with one another. However, in many cases these populations never get dense enough to compete for resources.

In benign environments, natural enemies tend to be much more effective (Connell, 1971) and most colonists are eaten. This tends to reduce competition and also to prevent the growth to an invulnerable size of the young dominants.

If the populations of grazers or predators are not reduced by some external event, they are capable of keeping the patch in this state of continual recolonization (the cycle between steps 3 and 4c).

However, if some unpredictable event, such as a short spell of bad weather or an attack by their own predators or pathogens, reduces the population of these natural enemies, the prey will have a period of good survival and growth. This then allows whichever dominant species happens to be present to grow to an invulnerable size (step 5c). Which, if any, do so depends upon which natural enemy is reduced and whether the reduction lasts for a long enough period. Once the prey reaches invulnerable size, it excludes or displaces other organisms by further growth (steps 5c to 6). The situation then returns to the original state (steps 6 to 1) as “sheltering” species colonize the area beneath the dominant.

In intermediate environments there is less mortality from harsh weather and natural enemies are less effective, so that the young of dominant species more readily escape being eaten. Thus these young dominants may reach high population densities and begin to compete with one another. The eventual winner, i.e., the dominant that eventually fills the space, is likely to be the one able to displace the others during a period of competition (steps 4b and 5b).

Which species of dominant will succeed in filling the vacated patch depends upon several things. For example, in benign regions such as the lower seashore there are more species of predators, and some,

such as starfish, are quite large and able to eat grazers and smaller predators as well as the dominant sedentary animals (Paine, 1966; Menge, 1972). Thus starfish tend to reduce both animal dominants and grazers. Plants should therefore be favored, since both their competitors and their natural enemies are being reduced. This may be the reason why, in temperate latitudes over the world, plants rather than animals are the dominant organisms covering the lower seashore. They form the “sublittoral fringe” in Stephenson and Stephenson’s (1949) universal scheme of zonation. In contrast, at middle shore levels, large predators such as starfish are less common; the main predators are muricid snails. They feed much more heavily on sedentary animals such as mussels and barnacles than on grazing molluscs, so that grazers are less likely to be reduced than they were at lower shore levels. This means that both plant and animal dominants are under attack, so that no a priori prediction can be made as to which will succeed in filling the vacated patches of rock surface. Barnacles, mussels, tube worms, oysters, and various algal species—all may occur as dominants in middle shore zones.

#### **What Determines Realized Niches and Community Structure?**

The distribution and abundance in which one finds a species, as opposed to its potential area and population size, is obviously not determined solely by competition. Therefore the variables that constrain the realized niche of a species

within its fundamental niche need not, as defined originally by Hutchinson (1958) and more recently by Vandermeer (1972), be limited to competitive interactions.

A major distinction was made earlier between species that reached a size much larger than their predators and those that did not. However, many species occur in both categories. A young member of a large species must spend some time in the latter category when predators are larger than it is. Even birds and mammals are vulnerable for a short time during infancy, and other groups may spend a much greater proportion of their lives in a vulnerable state. In addition, small prey are usually unattractive to much larger predators. Thus at any one time there is a restricted range of sizes of predators willing and able to attack an individual. As an individual grows, it may be attacked by a series of ever larger predators, or by predators operating in larger social groups.

Another important assumption underlying the present model is that predators attack with less intensity as physical conditions become harsher, i.e., more severe, variable, or unpredictable. Evidence supporting this generalization comes from gradients across the edges of lakes or the seashore, or from comparisons such as those between deep and shallow alpine ponds or between tropical and temperate latitudes, e.g., that nest predation of juvenile birds is greater in tropical than in temperate latitudes (Ricklefs, 1969; also data of G. Orians quoted in MacArthur, 1972, p. 218). Although further evidence is clearly desirable, this generalization seems to apply to a wide range of species.

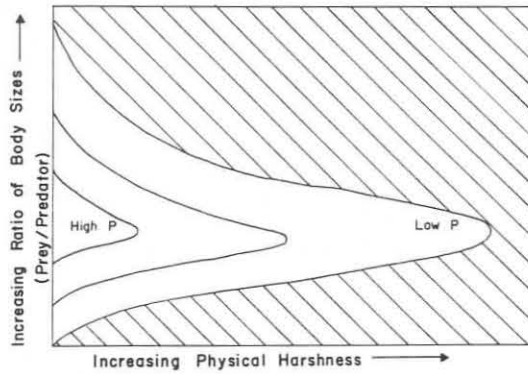
Thus we have found two relationships to be of prime importance: 1) the change in vulnerability of prey as its size varies in relation to that of the predator, and 2) the change in intensity of predation as physical conditions vary.

The first of these applies if prey and predator are to live intermingled together. The prey must be either so much smaller than the predator as to be economically unattractive, or so much larger as to be impossible to attack successfully. The size of either predator or prey refers to the operational unit, whether it be an individual or a pack.

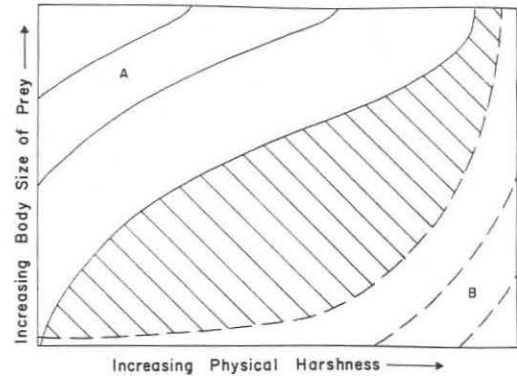
The second relationship is important for prey that do not grow large enough to escape their predators. Then prey must have a refuge from predation. One way this may occur is when predation diminishes as physical harshness increases; the prey may then evolve tolerance to physical regimes too harsh for the predator to attack effectively.

These points are combined in a diagrammatic way in Figures 2 to 5. Each of these represents a surface of varying probability of mortality per unit time, showing "contours" of equal probability. The shading indicates a region of very low probability of mortality. A gradient from left to right in all the figures represents increasing harshness of the physical regime, such as would obtain for a marine species from low to high levels in the intertidal zone. A gradient from bottom to top on the figures represents increasing body size of the prey.

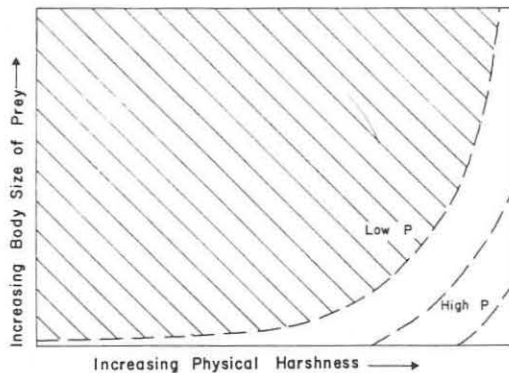
Figure 2 indicates the probability of being killed by a predator under different physical regimes and body sizes. Let us



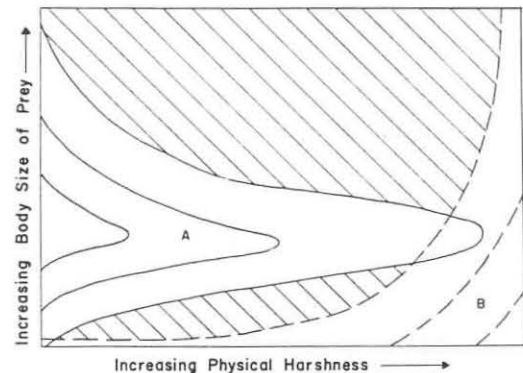
**Figure 2** Mortality due to predation under different physical regimes and body sizes. A point on the surface represents a particular probability  $P$  that a prey individual will be killed by a predator per unit time. The curves are contours of equal probability, high toward the left, the shaded region being one of very low probability of mortality from predation. A gradient from left to right represents increasing physical harshness. A gradient from bottom to top represents increasing relative body size of prey compared with predator.



**Figure 4** Mortality due to both predation and physical conditions, for prey that are small in relation to the size of their predators. The solid curves in region A represent probabilities of mortality from predation, as in the lower portion of Figure 2 with the scale expanded. The dashed curves in region B represent probabilities of mortality from physical factors, as in Figure 3. The shaded region represents a region of very low probability of mortality. See Figure 2 for more explanation.



**Figure 3** Mortality due to the direct effects of harsh physical conditions on prey of different body sizes. The gradients and curves are explained in Figure 2. A point on the surface now represents the probability  $P$  that a prey individual will die due to harsh physical conditions per unit time.



**Figure 5** Mortality due to both predation and physical conditions, for prey that grow to a large size in relation to the size of their predators. The curves for mortality from predation (solid lines, region A) are taken from Figure 2, those for physical effects (region B) from Figure 3. See Figure 2 for more explanation.



examine the situation in which the prey is relatively much smaller than the predator, i.e., as in the lower portion of the figure. Along any horizontal line, with a constant ratio of body sizes of prey and predator, the probability of mortality from predation decreases toward the right as the physical conditions become more harsh, because of a progressive reduction in the period of activity of the predator. Along a vertical line, representing a particular degree of physical severity, the probability of mortality increases upwards, as the prey become relatively larger. The reason is that very small prey are usually not eaten by a large predator; they are ignored, or not caught by the meshes of its filter, etc. Presumably there is a size of prey below which there is too low an energy return for the effort expended. These two tendencies cause the contour lines of equal probability of death to slant upwards to the right in the lower portion of Figure 2.

In the upper part of Figure 2, the prey are relatively larger. As before, along any horizontal line the probability decreases as the physical regime becomes steeper. However, along a vertical line at a particular physical regime, the probability of death decreases upward. As a prey individual grows, it becomes too large for a particular predator to attack. This also tends to reduce the number of species of predators that can attack it. These tendencies cause the contour lines to slant downwards to the right.

The shape of the contour lines would vary with different combinations of prey, predator, and physical regime. I have drawn them as they probably apply to the

species on rocky seashores. The situation in Figure 2 applies to predators and prey that have similar physiological characteristics, for example, marine organisms. In other instances, they may have quite different physiologies. For example, along shores of lakes or oceans, land animals feed on aquatic species. In this case, a mirror image of Figure 2 would be appropriate, since as the physical regime becomes less severe for the aquatic prey (toward the left), it would become more severe for the terrestrial predator.

The effect of the direct action of physical conditions on organisms of different sizes is shown in Figure 3. Along a horizontal line the probability of death per unit time increases toward the right. Upward along a vertical line the probability decreases since, as an individual grows, it becomes less vulnerable to the physical environment. These trends cause the contour lines of equal probability to slant upwards to the left. Again, the shape of the curves will depend upon the characteristics of the species and physical regime.

In Figures 4 and 5 I have combined the first two diagrams to illustrate the effect both of predators and of different physical regimes on the mortality of the prey. Figure 4 represents small prey, so uses only the lower portion of Figure 2. When prey are very small, they tend to be ignored by larger predators so that mortality is due mainly to physical harshness. As prey grow, they escape this hazard except where conditions are very severe. In very benign conditions, larger prey soon attract the notice of predators that tend to be active much of the time. In conditions of

intermediate severity, they escape the attentions of the less active predators for a longer time, and having passed the very young stages at which they are vulnerable to variations in physical conditions, they may be safe for a while. If local population densities are high enough, competition may take place during this interval before predation begins to reduce the populations.

Figure 5, which combines most of Figure 2 with Figure 3, represents the situation in which the prey grow to a relatively large body size. Once they have grown large enough to be less vulnerable to physical factors, they may or may not be safe from predators for a short while, but soon are attacked. However, if they survive long enough, they may reach an invulnerable size. (These diagrams do not take into account the fact that prey eventually become vulnerable again in old age.)

The situation in Figure 4 is exemplified by the two species of barnacles that competed only at intermediate intertidal levels in Scotland (Connell, 1961b). After eliminating *Chthamalus* in competition, *Balanus* was eaten by predatory snails, except in a refuge high on the shore. *Balanus cariosus* fits both Figures 4 and 5, depending upon the relative size of its predators. With small predators it is able to grow too large to be attacked (Figure 5), but with the large starfish it fits Figure 4. Many prey species probably pass through a similar series of ever larger predators.

Species of prey that never grow very large compared with their predators, such as the aquatic plankton or small land

plants or animals, are represented by Figure 4. Large plants and animals would be more closely represented by Figure 5.

### Summary

The distribution and abundance of a species are ultimately determined by tolerances to extremes of physical conditions, but a species is usually limited to a smaller range of habitats and population size by interactions with other organisms. The evidence reviewed in this paper, taken mainly from controlled field experiments on invertebrates and plants, suggests that many species seldom reach population densities great enough to compete for resources, because either physical extremes or predation eliminates or suppresses them in their young stages.

Species may sometimes escape these hazards to reach high densities in various ways. One way is through large size, which reduces vulnerability to harsh weather and predation, but the problem for a young individual is to reach a large enough size before it is killed. Strong parental care helps as in many vertebrates, but offspring without care will escape only during occasional reductions in predation or harsh weather. Such escapes may produce widely spaced "dominant year-classes." Once they reach large size, they may compete for resources and suppress smaller individuals. Examples are forest trees, large sessile aquatic animals, etc. A model of this situation is presented.

Second, some species can never grow so large as to escape predation. They may escape for a while if they are too small

to be attractive to the predator, and they may compete then. However, as they grow larger, they will be eaten unless they have a refuge where they are safe. If their habitat is patchy, e.g., small lakes or islands, they may colonize some patches before the predators reach them. Most smaller species have a refuge, permanent or temporary.

Since predation seems to be more intense in more benign physical conditions, competition should be prevented more regularly in more benign regimes. Escapes from predation and subsequent competition would be more likely in harsher regimes.

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